

## GROWTH RATE, LONGEVITY AND MAXIMUM SIZE OF *MACOMA BALTHICA* (L.)

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*Macoma balthica* (Linnaeus, 1758) has long been recognized as a dominant species in marine bottom communities ringing the boreal North Atlantic Sea and in the Arctic Seas (Thorson, 1957). Coan (1971) has recently synonymized *Tellina inconspicua* Broderip and Sowerby with *M. balthica* extending the range of this taxon into the North Pacific as far south as San Francisco Bay. Here the species is less dominant due probably to the very large number of other *Macoma* species in this region. Such an unusually extensive geographic range affords a rare opportunity to study the way one species adapts to widely varying climatic conditions.

A wealth of material on fundamental aspects of the life history of *M. balthica* has appeared over the past decade correcting a previous paucity of information. Two of these aspects, its growth rate and longevity, have been found to vary widely. Most workers (Vogel, 1959; Segerstrale, 1960; Lavoie, Tremblay and Filteau, 1968; Lammens, 1967; Semenova, 1970; R. H. Green, in preparation) have used annual rings produced by a cessation of growth during the winter to determine age and growth rate. In populations from Massachusetts to Chesapeake Bay, however, these bivalves do not display these rings (McErlean, personal communication). Neither can the difference in successive modes in size-frequency distributions be used to age these animals, because there are usually only two peaks— young of the year and adults. Since rates vary widely, I studied a population of this species at Rand Harbor, Falmouth, Massachusetts to determine growth rate and longevity in a southern population.

### METHODS

Sixty specimens of *M. balthica* ranging from 6 to 25 mm in length were measured to the nearest 0.1 mm using vernier calipers and tagged with numbered squares of adhesive tape glued to the left valve with a drop of fast-drying jeweler's cement. The India-ink numbers were protected by a coat of clear nail polish. The bivalves were then released (March 16, 1970) into a large wooden box (38 × 58 × 13 cm) filled with native sediment and placed flush with the sediment surface at one foot below mean low water (MLW) in Rand Harbor. The box was removed seasonally (May 21, August 13, November 27, 1970 and March 31, 1971), and the tagged animals were carefully screened from the sediment, measured and replaced within 12 hours.

Since variation in biomass/m<sup>2</sup> at a particular site may cause differences in growth rate, both the natural density and size distribution of *M. balthica* were

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examined at Rand Harbor. In October 1969 nine samples 62.5 cm<sup>2</sup> in area were taken to 15 cm depth at each of four stations along a transect extending from the salt marsh to one foot below MLW. All specimens of *M. balthica* were sieved from the sediment, counted and measured. Here as elsewhere (Segerstrale, 1960), the size distribution was found to vary with water depth, making improbable the existence of a "usual" size distribution. Therefore animals for this study were selected so that all lengths found at Rand Harbor in March 1970 would be well represented. Densities ranged from 184/m<sup>2</sup> at one foot below MLW to 492/m<sup>2</sup> at MLW in October 1969 so the experimental density of 272/m<sup>2</sup> was well within the natural range for this site.

*Macoma balthica* burrows deeper as it grows (Lammens, 1967; Gilbert, 1969); spat live in the top 1 mm while the largest adults can live up to 18 cm deep. Since the box was not this deep, a controlled experiment was run in July 1970 to determine if this or other factors affected growth. Two sets of 12 bivalves of equal length ( $\bar{x} \pm 1$  s.d. =  $11.7 \pm 2.1$  mm;  $11.9 \pm 2.1$  mm;  $t_{22} = 0.233$ ) were tagged as above. One set was released in a small box (38 × 28 × 13 cm) in the manner described above and the second in a comparable area of undisturbed sediment marked off by a bottomless frame (38 × 28 cm). It was hoped that control animals would resume their normal living position, yet not move beyond the confines of the frame. Sizes were small and density low so that optimal growth could be observed. Three weeks later the animals were recovered and measured as above.

The dry-weight biomass and dry shell weight of 14 animals collected at Rand Harbor on May 11, 1970 and 23 collected at Sagadahoc Bay, Georgetown, Maine, on January 1, 1972 were determined by carefully removing all flesh from the shell and drying tissues and shell separately for 24 hours at 70° C. The animals from Rand Harbor were separated on the basis of gonadal development; eight had ripe gonads and six had recently spawned. Those from Sagadahoc Bay had very small gonads if present. The caloric content per ash-free gram of dry-weight biomass was determined for eight animals from Rand Harbor (four collected on May 11 and four on August 28, 1970) using methods and a calorimeter described by Phillipson (1964).

## RESULTS

In the controlled experiment recovery was low; nine from the box and six from under the open frame. This is probably due to two factors: First, evidence of green crab and *Urosalpinx cinerea* predation, crushed and bored shells in the presence of both species, was abundant during this month and, secondly, several bivalves were probably missed due to the difficulty of removing all the sediment from the area under the open frame to a depth of 15 cm. The mean initial lengths of the recovered bivalves were still not significantly different ( $\bar{x} \pm 1$  s.d. =  $11.05 \pm 0.48$  mm;  $11.69 \pm 0.45$  mm;  $t_{13} = 0.179$ ). The mean growth was not significantly affected by enclosure but the animals in the open frame grew somewhat more (open frame  $\bar{x} \pm 1$  s.d. =  $3.7 \pm 0.79$  mm; box  $\bar{x} \pm 1$  s.d. =  $2.4 \pm 0.15$  mm;  $F_{1,13} = 2.54$ , n.s.).

Mortality in the year-round study was 15% ( $n = 9$ ) and varied little by recapture date (Fig. 1, insert). There was no emigration or loss due to predation,

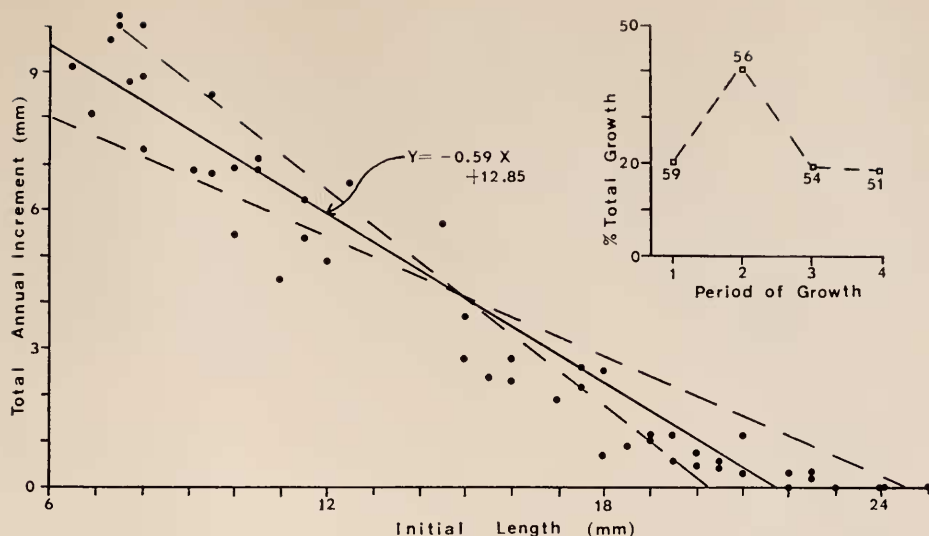


FIGURE 1. Total annual increase in length of 51 specimens of *M. balthica* of varying initial lengths. Dotted lines indicate 95% confidence intervals for the slope. Insert: seasonal growth as a percentage of the total annual growth; sample sizes are indicated for each period of growth (1 = 3/16–5/21/70; 2 = 5/21–8/31/70; 3 = 8/13–11/27/70; 4 = 11/27/70–3/31/71).

although the bivalves in the neighboring experiment suffered heavy losses. *M. balthica* living throughout the year ( $n = 51$ ) was used in the calculations below. Although the original number of marked bivalves is low for the mark-and-recapture method, the ability to recapture every individual at each sampling period resulted in data comparable to that resulting from studies using free-ranging animals (*e.g.* Frank, 1969).

Growth occurs steadily throughout the year except during the summer when it accelerates sharply (Fig. 1). The summer growth period starts around May, when this population spawns and evidently ends abruptly at the beginning of August, when gonadal regeneration begins (Gilbert, unpublished data). The relationship between initial length ( $X$ ) and total annual increment ( $Y$ ) can be expressed by the equation  $Y = -0.59X + 12.85$  with a 95% confidence interval for the slope of  $-0.64$  to  $-0.54$  (Fig. 1).

The growth of the 1970 year class in the present study was followed by measuring the small, unmarked specimens of *M. balthica* first found in the box in August where they probably settled as spat. The wide size range (3.4–7.4 mm) of these juveniles in August suggests that spatfall occurs from May into the summer. They were returned to be censused again in November when they had attained sizes from 7.0–12.7 mm ( $\bar{x} = 9.66$  mm;  $s.d. = 1.61$ ;  $n = 22$ ).

A growth curve (Fig. 2) was constructed for the population at Rand Harbor assuming that the observed rates apply to the whole population and that the climate in 1970–71 was typical. Surface sea water temperature data taken at the Buzzards Bay light station show that 1970 was an average year; the mean 10-day average for 1970 was  $10.56^{\circ}\text{C}$  while the overall average for the years 1956–70

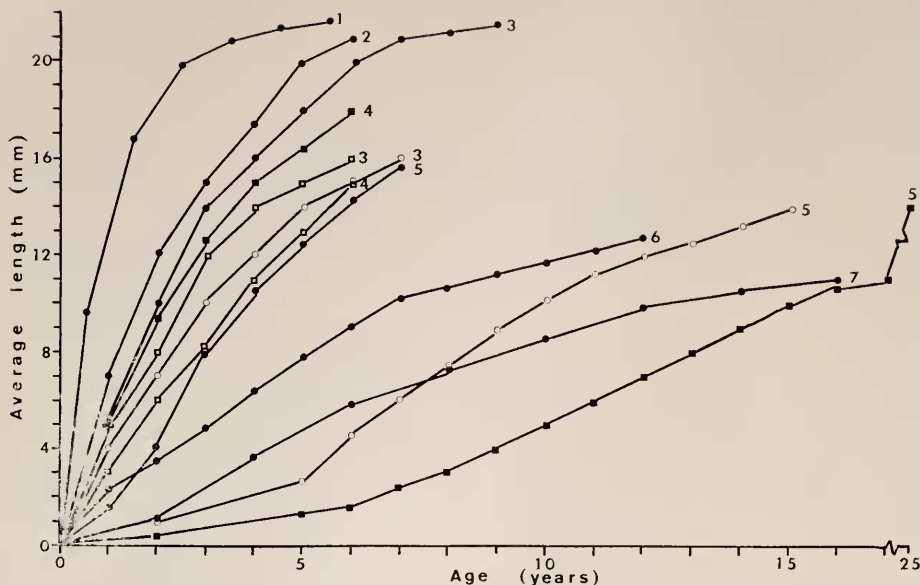


FIGURE 2. Growth curves of populations of *M. balthica* in different localities. The locations are: (1) Rand Harbor (-0.3 m); (2.) Wadden Zee, The Netherlands; (3.) (Vogel) North Sea (filled circle), Kiel Bay (open square), Gulf of Finland (6 m; open circle) (4.) Hudson's Bay, 1.1 m (filled square), MLW (open square); (5.) Gulf of Finland (Segerstrale), 3 m (filled circle), 20 m (open circle), 35 m (filled square); (6.) St. Lawrence River; (7.) Kandalski Bay, White Sea. For further details see Table I.

was 10.27° C (Chase, 1972). The curve was constructed in segments: the growth for the first  $\frac{1}{2}$  year is the average growth of the spat found in the box in August and measured again in November; later segments were constructed using the relationships in Figure 1. The resulting curve shows that at Rand Harbor, *M. balthica* attains most of its adult length within the first two years of its life. Then growth tapers and finally ceases for an unknown period once a size of 22+ mm has been reached. This study and others' findings suggest a total life span of 6-10 years in Rand Harbor.

There were no significant differences in the following relationships:  $\log_{10}$  dry weight biomass *versus*  $\log_{10}$  shell length in animals with ripe *versus* those with spawned gonads at Rand Harbor;  $\log_{10}$  shell weight *versus*  $\log_{10}$  shell length and  $\log_{10}$  dry weight biomass *versus*  $\log_{10}$  shell length in Maine *versus* those relationships in Massachusetts. The combined regression of dry shell weight (Y) on shell length (X) was  $\log_{10} Y = 2.98 \log_{10} S - 0.23$  and that of dry weight biomass (Y') on shell length (X) was  $\log_{10} Y' = 3.05 \log_{10} X - 1.12$ . The combined regression coefficients (2.98; 3.05) were not significantly different indicating that these two dimensions show a similar allometric growth with a constant of allometry of approximately 3 (Simpson, Roe and Lewontin, 1960). There was no significant difference between the mean caloric content of animals collected in May and August; the average of the eight replicates was 4.049 kcal/ash-free g. All statistics were calculated according to Sokal and Rohlf (1960).

DISCUSSION

In *M. balthica* data presented here suggest that maximum size and growth rate decreases and longevity increases with increasing latitude and relatedly cooler temperatures and shorter growing seasons (Table I and Fig. 2). Nutritive conditions and changes in salinity have formed the basis of earlier theories accounting for the variability in the maximal size. Segerstrale (1960), finding that both size and temperature decreased with depth (Sta. I-XLIV), concluded that, since the magnitude of temperature change was not sufficient to explain the decrease in size, growth was stunted because the available food becomes nutritively poorer in deeper waters (page 62). Segerstrale's temperature data, however, indicate a considerable lag in the warming of deeper waters and a progressively shortened

TABLE I

*Comparison of temperature, longevity, and maximum size of Macoma balthica at various locations*

Locality	°N. lat.	Average longevity (years)	Max. size (mm)	Water temperature (°C)	Source
Patuxent River	38-39				
Sta. 4			31-32	19 (Average spring	McErlean, 1964; Pfitzenmeyer and Drobeck, 1963
6			25-26	17 temperature,	
8			27-28	14 Potomac River)	
10			27-28	10	
Rand Harbor, Buzzards Bay, Massachusetts	41 30'	6-10	26	14 (May 1970)	Gilbert
Wadden Zee, Den Helder, Netherlands	53	6	23	14 (May 1963)	Lammens, 1967
Gulf of Finland, Tvarminne, Finland	60		(mean max.)		Segerstrale, 1960
Sta. I (3m)		7-8	20.9	6-11 (May 1927-32)	Vogel, 1949
Sta. XXVI (20 m)			18.4	1-5 (May 1929-32)	
Sta. XLIV (35 m)			17.3	1-4 (May 1929-32)	
North Sea		9	22		
List, Sylt, and Norderney, Germany	55				Vogel, 1949 Vogel, 1949
Kiel Bay, Germany	54 30'	6	15		
Gulf of Finland, Tvarminne, Finland (6 m)	60	7	15		
Kandalski Bay, White Sea, USSR	66	25-30	17	7 (May 1962)	Semenova, 1970
St. Lawrence River Cacouna, Quebec	48	12	13	4 (May 1967)	Lavoie <i>et al.</i> , 1968
Hudson's Bay Churchill, Manitoba	58 46'				Green, in prepara- tion
1.1 m		8	17	-5 to 10 (Average May)	Stephen, 1931 and 1938
MLW		?	13	9 (July 5, 1970)	
Aberlady Bay, Firth of Forth, Scotland	56	2	8-9	12 (Mean air temp. May to Sept.)	

growing season for benthic fauna. Vogel (1959) found decreasing size with decreasing salinity in a series of stations from the North Sea into the Baltic Sea, while McErlean (1964) also found a decrease in size, but with an increase in salinity in the Patuxent River estuary in Chesapeake Bay; neither author presented temperature data. Pfitzenmeyer and Drobeck (1963), however, present temperature and salinity data for stations in the Potomac River, adjacent to the Patuxent. When stations of similar salinities in these two rivers are compared, it is evident that both temperature and maximum size increase as salinity decreases. In any case, it is very unlikely that salinity had an important effect, considering the very wide salinity tolerance of this species (Lavoie, 1970; Bagge, 1965). Thus both formerly conflicting data and variable maximal sizes in this species can be most simply explained as a function of the hydroclimate: with warmer temperatures and a longer growing season, a larger size is attained. The one exception seems to involve a transient population in Scotland (Stephen, 1931) that barely reaches a size that is reproductive at Rand Harbor. Hydrographic conditions and selective predation have been shown to remove size classes shortening the life span at other sites (Lavoie, 1970; Semenova, 1970). Such factors may be acting on the Scottish population.

Growth rate and longevity are also related to temperature: at higher temperatures *M. balthica* grows faster, but seems to have a shorter life span (see also Segerstrale, 1960; R. H. Green, in preparation). The influence of temperature on growth rate and maximum size is evident in Green's study (number 4 on Fig. 2). Although food availability is similar, specimens of *M. balthica* at 1.1 m above MLW grew faster and reached larger sizes than those at MLW; the former are exposed about 37% of the time to 15–18° C air temperature during July and August while the latter are usually covered by cold arctic water. A similar pattern is found in intertidal populations of *Mytilus californianus* where the growth rate of an Alaskan population is lower than Californian ones (Dehnel, 1956). Studies on temperature compensation in other molluscs have shown that measures of metabolic rate, such as rate of heart beat and oxygen consumption, are higher in cold-adapted animals, *i.e.* those living at the northern end of a species range or at the lower end of the intertidal (Segal, 1956, 1961). Cold-adapted *M. balthica* may therefore be expending more energy on respiration and less on growth than warm-adapted individuals.

At Rand Harbor, most *M. balthica* larger than 22 mm were not observed to grow during the study year (Fig. 1). Elsewhere they continue to grow throughout the life span but so slowly that 22 mm is never reached despite life spans up to 25 years (Fig. 2). Although a smaller ultimate size may be intrinsic at more northerly sites, the shape of the growth curves disputes this conclusion. Although the inverse relationship between longevity and growth rate is well documented, the reason why it occurs is still unknown.

*Macoma balthica* and *Scrobicularia plana*, a larger, related, also deposit-feeding species that often replaces *M. balthica* in more saline flats (Spooner and Moore, 1940), exhibit the same allometry of size. Hughes (1970) found an average regression coefficient of 3.00 for the relationship of  $\log_{10}$  dry-flesh weight (g) to  $\log_{10}$  shell length (mm) and  $3.41 \pm 0.82$  for  $\log_{10}$  shell weight to  $\log_{10}$  shell length. *Scrobicularia plana* also has a low caloric content (5.197 kcal/ash-free g; Hughes,

1970). Slobodkin (1962) considered *Ensis minor* with a caloric content of 3.5 kcal/ash-free g to be an exception to other animals examined which fell in the higher range of 5.5–7.5 kcal/ash-free g. The evidence seems to be mounting, however, that bivalve mollusks as a group have a low caloric content perhaps due to their low lipid content (Hughes, 1970).

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#### SUMMARY

1. Growth rate and longevity were determined for a population of *M. balthica* at Rand Harbor, Falmouth, Mass., using a modification of the mark and recapture technique that allowed all marked individuals to be followed throughout a year. Dry weight biomass, dry shell weight and caloric content were also determined.

2. Caloric content is 4.049 kcal/ash-free g. Dry weight biomass and dry shell weight were found to have a similar allometric growth with a constant of allometry of approximately 3 when measured against shell length.

3. The bivalves were discovered to grow year round with the peak period of growth occurring from May to August. A negatively linear relationship between initial length (X) and total annual increment (Y) was found ( $Y = -0.59 X + 12.85$ ).

4. The growth curve for the Rand Harbor population revealed that within the first two years of life, *M. balthica* attains most of its total length. Growth ceases once a maximum size of 22–25 mm is reached and total longevity is estimated to be 6–10 years.

5. These results were compared to other studies and the theory that maximum size, growth rate and longevity are controlled by temperature presented and discussed.

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